

Habitat availability and depth-driven population demographics regulate reproductive output of a coral reef fish

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Abstract. Global habitat decline may displace organisms from optimal environments, increasing reliance on ecosystems with lower habitat suitability and availability. For coral reef fishes, potentially marginal mesophotic coral ecosystems (~30–150 m) may be buffered from anthropogenic stressors; however, variation in habitat quality across depths can alter population demographics, reproductive output, and subpopulation size, potentially restricting the ability for peripheral habitats to support declining populations through larval supply. This study incorporated population density, benthic habitat, and depth-stratified population demographics to assess bicolor damselfish (*Stegastes partitus*) subpopulation reproductive output from a broad geographic region encompassing the known depth distribution of the species, including coral reefs in the Florida Keys (0–35 m depths) and mesophotic reefs (~60–90 m) at Pulley Ridge (PR) on the west Florida Shelf. Results indicated that densities of bicolor damselfish peaked in mid-shelf (10–20 m) and deep-shelf (20–30 m) habitats, and subpopulation sizes and reproductive output peaked at mid-depths (10–20 m) in the Florida Keys and declined as depth increased. Subpopulation egg production was affected by differences in demographics across depths, including fish size, sex ratios, and a lower probability and frequency of spawning in deeper habitats. Despite low population densities on mesophotic reefs, the expansive reef area at PR resulted in an estimated subpopulation size that comprised ~14% of the population in the study region, and ~9% of the total reproductive output, indicating that peripheral mesophotic reefs may be sources of larvae that can subsidize declining populations. Larval dispersal and population connectivity models used to inform ecosystem management should incorporate spatially explicit demographics across depth distributions and habitat availability that have substantial effects on egg production and larval supply.

Key words: coral reef; demography; distributions; ecosystem management; fishes; life history; marginal populations; mesophotic coral ecosystem; metapopulations; population dynamics; reproductive output.

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INTRODUCTION

Metapopulation dynamics are regulated by export and import of individuals among spatially separated subpopulations with variable habitat quality, subpopulation sizes, and local demographic patterns (Jaquiéry et al. 2008, Cowen and Sponaugle 2009, Ferrer et al. 2015). For organisms

with distinct dispersal stages, such as most coral reef fishes, the degree of population connectivity among local subpopulations is determined by larval production, growth and survival of planktonic larvae, delivery and settlement of larvae to the reef environment, and postsettlement processes (Robertson et al. 1988, Schmitt and Holbrook 1996, Cowen and Sponaugle 2009). Reproductive output

defines the upper limit of larval production and supply prior to larval mortality or advection (Cowen and Sponaugle 2009), thus providing a method to evaluate the maximum potential larval contribution of a habitat to the larger metapopulation.

Habitat suitability and availability in combination with demographic parameters influence local reproductive output and larval contributions from a subpopulation. Across ecosystems, optimal habitats with high food and shelter availability and low predation often support large high-density populations (Wynne and Côté 2007, Hixon et al. 2012, Curtis et al. 2015) with higher condition individuals (Jones 1986, Booth and Hixon 1999, Munday 2001). For marine fish, habitat variability can also differentially affect juvenile and adult distributions (Dahlgren and Eggleston 2000, Kimirei et al. 2015), and the growth and size of individuals (Ruttenberg et al. 2005). Fish density and age distributions often vary temporally and spatially as a result of local mortality rates and predation pressure (Shulman and Ogden 1987, Johnson et al. 2014), or dynamic oceanographic processes that bring pulses of larvae to, or advect larvae away from settlement habitats (D'Alessandro et al. 2007, Hogan et al. 2012). Such spatiotemporal patterns of population structure result in variable subpopulation reproductive output (Ruttenberg et al. 2005, Carter et al. 2014), and at larger spatial scales, the amount of available habitat and local demographic parameters determine regional larval quality and production (Holbrook et al. 2000, Munday 2000, Johnson 2007).

Effective management of declining ecosystems (Hoekstra et al. 2005), such as vulnerable coral reef habitats (Pandolfi et al. 2003), requires an understanding of source–sink dynamics and the potential larval contributions of individual habitats or subpopulations to the larger metapopulation. Habitat degradation may restrict species' distributions or push organisms into peripheral and marginal environments (Bongaerts et al. 2010, Davis et al. 2015) where lower habitat quality may limit reproductive output and larval production. For coral reef fishes, population demographics change rapidly across depth distributions from shallow to mesophotic depths (~30–150 m deep; Goldstein et al. 2016). As mesophotic reefs are often buffered from temperature fluctuations, physical disturbances such as storms, or from anthropogenic stressors such as fishing and

tourism due to habitat inaccessibility compared with shallower environments (Slattery et al. 2011, Lindfield et al. 2016), they have the potential to function as natural ecosystem refuges. Vertical connectivity of coral (Van Oppen et al. 2011, Serrano et al. 2014) and fish (Tenggardjaja et al. 2014) populations, high fecundity of mesophotic corals (Holstein et al. 2015), and similarities in taxa across depths (Kahng et al. 2010) suggest that shallow and mesophotic fish populations are connected through larval dispersal. However, mesophotic habitats at the periphery of coral reef ecosystems may be marginal environments for reef organisms. Population density and demographics that vary across geographic regions and depths may influence the refuge function of mesophotic coral reef habitats to supply larvae to degraded reefs (Brokovich et al. 2008, Lesser et al. 2009, Slattery et al. 2011).

The goal of this study was to identify spatial patterns of bicolor damselfish (*Stegastes partitus*) population distributions and incorporate depth-stratified demographic variation across the majority of the depth range of photosynthetic coral reefs to determine spatially expansive estimates of fish population reproductive output. An understanding of reef fish populations across multiple spatial scales contributes to our ability to evaluate the resilience of coral reef ecosystems, in particular, the capacity of peripheral habitats to safeguard viable subpopulations of organisms that could contribute to the recovery of stressed reefs through reproduction and larval dispersal. Enhanced understanding of the implications of spatially variable demographics to population dynamics can contribute to marine reserve design by identifying regions of high reproductive output that are potential larval source locations. Spatially explicit population size and egg production data are critical to biophysical modeling efforts that assess population connectivity, habitat value, and source–sink dynamics that are applicable to ecosystem assessments and to predicting population and ecosystem responses to environmental change and future disturbances.

METHODS

Study location

The coral reefs distributed around the southern Florida Peninsula are connected by the

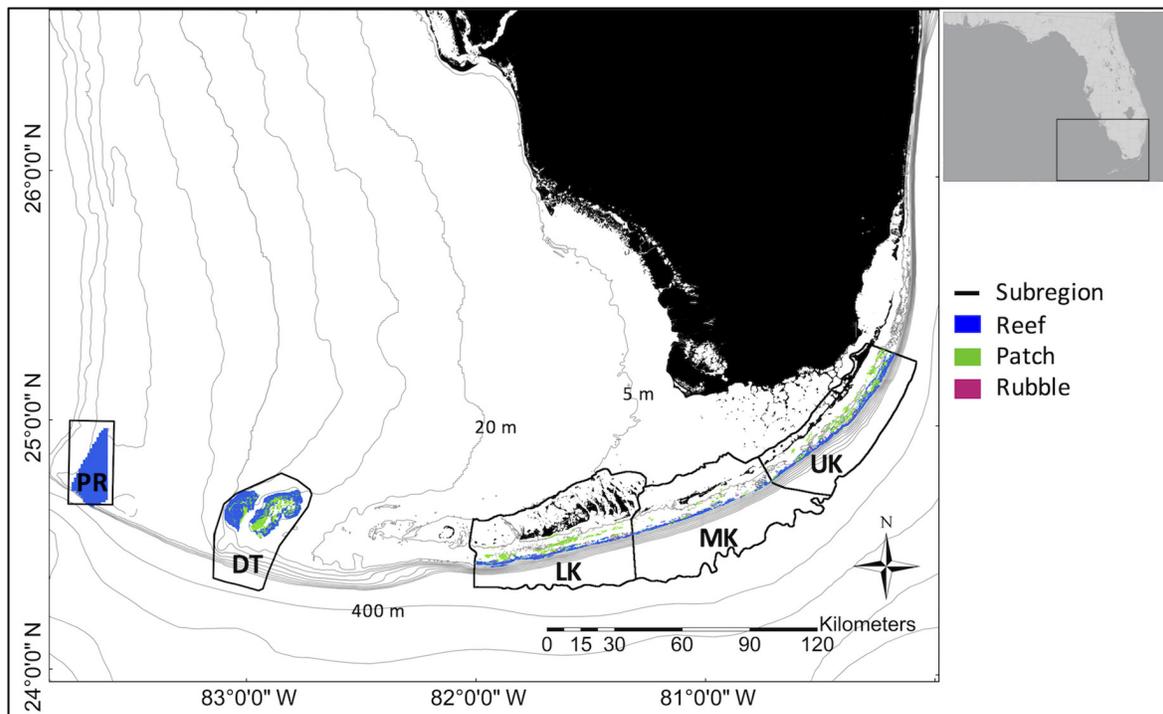


Fig. 1. Map of the Florida Shelf study region designating subregions (PR, Pulley Ridge; DT, Dry Tortugas; LK, lower Florida Keys; MK, middle Florida Keys; UK, upper Florida Keys), benthic habitat in the Florida Keys and DT, and probable reef habitat at PR. The rectangle polygon outline at PR designates probable reef habitat, and the blue polygon represents the NOAA-designated Habitat Area of Particular Concern (HAPC) with known scleractinian coral and fish habitat. Bathymetry contours are labeled at the 5, 20, and 400 m. Contours are 10-m intervals from 20 to 100 m, and 400-m intervals starting at the 400 m contour.

Florida Current, a major western boundary current that forms as the loop current flows out of the Gulf of Mexico into the Florida Straits, creating high potential for larval connectivity in the region (Qian et al. 2015). At the southern tip of the Florida Peninsula, the Florida Keys reef tract stretches for ~300 km with the Dry Tortugas (DT) to the west (Fig. 1). Pulley Ridge (PR) is a mesophotic hermatypic coral reef habitat located at depths of ~60–100 m along the west Florida platform, with estimates of nearly 60% of the benthic habitat occupied by live biota in the southern portion of the ridge (Reed 2016). Southern PR includes a National Oceanographic and Atmospheric Administration (NOAA)-designated Habitat Area of Particular Concern (HAPC) with known scleractinian coral and fish habitat (Fig. 1; Cross et al. 2005, Reed et al. 2014). Recent studies show that the region west of the PR HAPC also has hard bottom habitat with

scleractinian coral and reef fishes (Reed et al. 2014).

Study approach

Numerous data sets and sources were used to assess depth distributions, population densities, and reproductive output of bicolor damselfish. To calculate reproductive output for the entire reef habitat in the Florida Keys and mesophotic reef habitat at PR, we sequentially layered and refined analyses using each data set to obtain estimates of depth-stratified and subregional reproductive output (Fig. 2). The base data sets included benthic habitat and fish count visual SCUBA surveys (depths of 0–35 m) in the Florida Keys (UK, upper Florida Keys; MK, middle Florida Keys; LK, lower Florida Keys) and DT, and remotely operated vehicle (ROV) fish and benthic habitat surveys in deeper habitats (28–81 m deep) in the DT and PR. These data sets

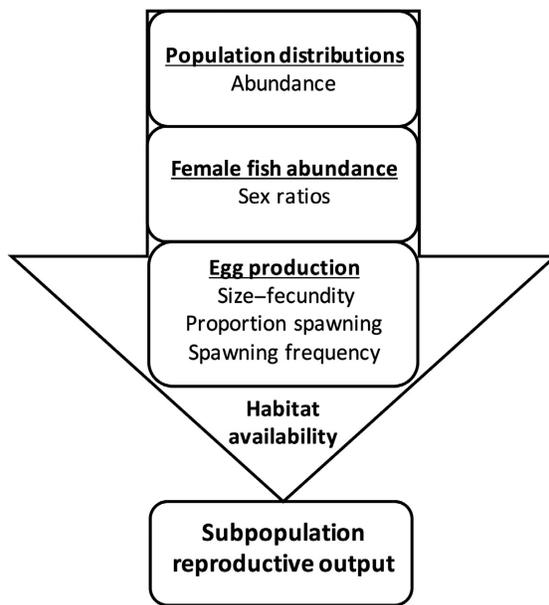


Fig. 2. Schematic of the data analysis approach. Sequential layers of analysis are listed from top to bottom with descriptions of the goal and data set used for each layer of analysis.

were used to obtain spatially explicit density distributions of bicolor damselfish in reef habitats across depths and regions. To modify densities to include only female fish, and incorporate empirical depth-stratified size distributions, we applied sex ratios and length distributions obtained from random fish collections at discrete depth strata (shallow shelf <10 m, deep shelf 20–30 m, and mesophotic 60–70 m) to population densities. Fecundity is size dependent; thus, the regression relationship between fish size and batch fecundity was used to convert depth-specific densities and size distributions into estimates of reproductive output per unit area. Fish collections and histological slides of ovaries were used to further refine reproductive output estimates by calculating the proportion of female fish that spawn from each depth stratum, and incorporating a temperature-dependent spawning rate to estimate weekly reproduction (Ganias et al. 2007; Goldstein et al. 2016). Population density data, depth-specific demographics, and benthic habitat data were then used to estimate depth-stratified weekly egg production for the entire reef habitat of the Florida Keys and mesophotic reef habitat at PR.

Population distributions

Abundance data sets.—Visual survey data for a 12-yr time period from 2000 to 2011 (NOAA National Marine Fisheries Service Southeast Fisheries Science Center) were used to assess bicolor damselfish population densities and distributions throughout the Florida Keys and DT at depths <35 m. Detailed visual survey methods are described by Bohnsack and Bannerot (1986) and Smith et al. (2011) and are only briefly summarized here. Data were collected during the summer months using a probabilistic sampling approach by dividing the region into primary sampling units (PSUs) of 200 × 200 m grid cells. Primary sampling units were randomly selected for fish count surveys conducted by SCUBA divers within a visual cylinder with a 7.5-m radius. If visibility was <7.5 m, the radius of the observation cylinder was modified to 4 m, and if visibility was <4 m, the survey was not included in the analysis. Divers recorded the count and minimum, median, and maximum estimated fish size by calibrating observations using a ruler attached to a rod, and triangular fish length distributions were calculated using length estimates (Bohnsack and Bannerot 1986, Smith et al. 2011).

To determine population distributions along the entire depth range of the species, bicolor damselfish densities and abundance were quantified using 176 ROV transect surveys (University of North Carolina Wilmington *Super Phantom S2*) on mesophotic reefs in the DT (28–58 m deep) and at PR (65–81 m deep). Surveys were conducted during daylight hours in the summer months of 2012 and 2013 (Reed et al. 2014). Sample locations were selected by digitally overlaying multibeam bathymetry maps with 1 × 1 km blocks (ESRI ArcGIS 10.0). A total of 33 random blocks were selected for the ROV surveys, typically with five independent 100-m ROV transects conducted within each block. Continuous digital video was obtained using a Sony standard-resolution, single-chip color video camera (410 × 380 pixels; 79° diagonal angle in water) with 12:1 zoom, and auto/manual focus that was angled ~20–30° down. Analyses were based on the latitude, longitude, and water depth at the start of each transect. Specific location and depth data were unavailable for 16 transects, and values were substituted with the mean latitude, longitude,

and depth of all transects within the same random block. Fish densities were calculated using a linear transect distance of 100 and a 5 m width field of view. Additional ROV survey details are described by Reed et al. (2014).

Spatial patterns of abundance.—To address spatial and temporal patterns in fish distributions, the 14 yr of visual and ROV survey data were separated into 3-yr time periods from 2000 to 2002, 2003 to 2005, and 2006 to 2008, and a 5-yr time period for the most recent years from 2009 to 2013 that incorporated visual and ROV surveys. Estimated lengths of bicolor damselfish observed during surveys were used to roughly separate fish counts into juvenile (≤ 5 cm total length, TL) and adult (> 5 cm TL) age categories based on a $\sim 50\%$ maturity of female fish at 5 cm TL (Goldstein et al. 2016), using a standard length (SL) to TL conversion ($TL = 1.2 \times SL + 0.5$, $r^2 = 0.99$; Goldstein and Sponaugle, *unpublished data*). For diver visual surveys, age categories were based on diver-estimated size categories, and for ROV surveys, age categories were determined based on measured TL of fish from diver collections in the DT (18% juvenile and 82% adult) and PR (22% juvenile and 78% adult). Analyses included only benthic habitat categories in which bicolor damselfish were present, designated as rubble, patch reef, and reef. The habitat categories included a combination of reef habitats with varying degrees of rugosity and complexity. For patch reefs, habitat categories included low-, mid-, and high-relief habitats. In reef environments, habitats included continuous and spur and groove reefs with low to high rugosity sub-categories (Appendix S1).

For diver visual surveys, bicolor damselfish juvenile and adult densities were calculated by averaging the bicolor damselfish density among all surveys within the same PSU to obtain an average PSU fish density/m². Average densities were then extrapolated to total PSU fish density (fish 0.04/km²). For ROV surveys, fish density/m² was calculated for each transect, and then extrapolated to 200 × 200 m² to match the spatial scale of the visual survey data set.

Remotely operated vehicle sampling methods have the potential to underestimate population densities in comparison with visual surveys (Andaloro et al. 2013); therefore, data sets were compared to determine whether the

two methods could be combined for analysis. Presence/absence calculations for diver visual surveys were based on replicated surveys within each 200 × 200 m PSU. An individual SCUBA diver survey encompassed a visual area of ~ 177 m² with an average of 2.6 surveys within each PSU. These calculations indicate that the probability of observing a bicolor damselfish during visual surveys in each PSU was based on ~ 460 -m² search area, compared to a 500-m² survey area for each ROV transect. Therefore, the search area for occurrence was similar between methods. Benthic habitat information associated with visual surveys was confirmed by SCUBA divers in contrast to the longer ROV transects that encompassed both reef and non-reef habitat. To correct for this discrepancy in sampling, we excluded three sample blocks that were outside of the known coral reef habitat at PR (Reed et al. 2014). The ability to combine survey methods was also verified by comparing bicolor damselfish densities from 2012 to 2013 from ROV surveys with 7 yr of visual survey data within an overlapping spatial area and depth range in the DT (Wilcoxon signed-rank test, $P > 0.05$).

To model and predict bicolor damselfish distributions throughout the entire study area, the influence of depth and location on bicolor damselfish density was assessed using hurdle models (pscl package; Zeileis et al. 2008, Jackman 2015, R Core Team 2016). Hurdle models incorporate a presence/absence logistic regression component and a count model component (Potts and Elith 2006). Following a positive observation, count data were modeled based on a negative binomial distribution that allows for overdispersion in the data set (Ver Hoef and Jansen 2007). Visual surveys by SCUBA divers were stratified to suitable habitat based on diver verification, whereas ROV surveys likely incorporated unsuitable environments. An underlying assumption of hurdle models is that occurrence and abundance are influenced by separate processes, suggesting that hurdle models are an appropriate method to model regions that encompass suitable and unsuitable habitats (Potts and Elith 2006). Neither latitude nor longitude accurately represents location along the curved reef tract (Fig. 1); therefore, survey locations were linearized by fitting a polynomial regression curve to the reef tract ($R^2 = 0.95$). Location was described by calculating

the arc length from the farthest west observation at PR, to the fitted value of the sample location along the curve (pracma package; R Core Team 2016). A location of 0 corresponds to the location farthest to the west, and the value increases as the sample location approaches the UK.

Separate hurdle models were fit for rubble, patch reef, and reef habitats because some benthic habitat types were restricted to particular depths, confounding habitat-stratified density analysis. Distributions were modeled using the square root of the depth, linearized longitude, and a polynomial depth term because the relationship between depth and abundance was not monotonic. Spatial autocorrelation for each model was addressed by plotting Moran's I correlograms of model residuals and assessing Moran's I standard deviate test statistics (ncf package; Dormann et al. 2007, R Core Team 2016). All model selection procedures started with the full model that included a squared term for depth and an interaction between depth and location. Sequentially simplified candidate models were compared based on Akaike information criterion (AIC; Akaike 1973). For model selection, AIC weights were compared among competing models with ΔAIC values < 2 (Burnham and Anderson 2002).

Female fish abundance

Predictions of female bicolor damselfish densities for the Florida Keys and PR were made using hurdle model results from the 2009 to 2013 time period to determine population distributions of reproductively mature females. These analyses focused on 2009–2013 based on the availability of demographic data (Goldstein et al. 2016), and because that time period had the broadest sampling depth range and most consistent coverage of the Florida Keys. Bicolor damselfish density predictions and bootstrapped 95% prediction intervals (1000 replicates calculated based on model response and Pearson residuals) were obtained using hurdle models for each habitat across the study region. Density predictions were then modified using the proportion of mature female fish from depth-specific sex ratios to obtain an estimate of female bicolor damselfish counts within each subregion and depth stratum. Density predictions were not made for rubble habitats based on low density

and low probability of occurrence of adult bicolor damselfish.

Depth-specific sex ratios were calculated using random fish collections from PR (60–70 m) from 2012 to 2014 and transect collections from shallow-shelf (0–10 m) and deep-shelf (>20–30 m) reefs in the LK from June to August 2013 and 2014 in which every fish observed along a 25×2 m transect was collected and sexed (Goldstein et al. 2016). Because transects and collections were not conducted on mid-shelf reefs (10–20 m), shallow-shelf data were applied to the mid-shelf visual survey counts. This convention was used for all further depth-stratified demographic analyses, and the choice was based on the decline in fish density at ~20 m depth (see *Results*), suggesting a habitat shift within that depth range.

For regional and depth stratum estimates of total population sizes, predictions were extrapolated to total habitat area in each subregion and depth stratum (shallow shelf: $0 < 10$ m, mid-shelf $10 < 20$ m, deep shelf: $20 \leq 30$ m, and mesophotic: 60–90 m) based on benthic habitat maps. For model predictions at PR, the area of the HAPC (350 km^2) was designated as reef, which may be an underestimate of the spatial extent of reef habitat in the region (Cross et al. 2005, Jarrett et al. 2005, Locker et al. 2010, Reed et al. 2014). Habitat maps in the Florida Keys had a 200-m^2 resolution, compared with 1-km^2 resolution at PR. Therefore, abundance estimates were arithmetically modified to match the spatial scale of benthic habitat information. Bicolor damselfish predictions per unit area (km^2) for each habitat type were calculated by dividing total abundance by the total habitat area of the subregion and depth stratum.

Egg production

Reproductive output is dependent upon population size and fish fecundity; therefore, we applied size–fecundity relationships to female fish density and population estimates to determine subregional egg production based on demographic characteristics. Precise size distributions were incorporated into reproductive output calculations using a positive linear relationship between fish size and fecundity. Fish collections at shallow-shelf (<10 m) and deep-shelf (20–30 m) sites in the LK, and from mesophotic reefs (60–70 m) at PR from June to August 2013 and 2014 were used to refine coarse size distributions from

visual survey data. All randomly collected mature female fish from shallow-shelf, deep-shelf, and mesophotic reefs were measured to the nearest 0.1 mm, and SL size distributions were applied to density calculations. The size distributions of mature female fish for each depth stratum were smoothed using a kernel density smoother, and the area under the curve was calculated to obtain proportions of the total number of female fish that were within 1 mm size bins (pracma package; R Core Team 2016). The depth-specific size proportions were applied to the predicted counts of female bicolor damselfish for each unit area for visual and ROV surveys, within each PSU in the Florida Keys and each 1-km² observation for PR.

The relationship between SL and batch fecundity for bicolor damselfish (batch fecundity = $265.02 \times \text{SL} - 5233.73$, $R^2 = 0.39$, adapted from Goldstein et al. 2016) was used to calculate potential reproductive output for each fish observed, and then extrapolated to population reproduction for a given unit of area. The population fecundity values were adjusted using calculations of the number of female fish spawning in each depth stratum during peak reproduction, based on the proportion of female fish collected that had ovaries with postovulatory follicles, or evidence of recent spawning (shallow shelf: 0.46, deep shelf: 0.29, and mesophotic: 0.33; Goldstein et al. 2016). The degeneration of postovulatory follicles is temperature dependent; therefore, the rate of postovulatory follicle degeneration based on mean temperatures from each depth stratum during the time period of the fish collections was incorporated into the analysis (Goldstein et al. 2016). The presence of postovulatory follicles indicated spawning within the last 2 d on shallow- and deep-shelf reefs, and within the last 3 d on mesophotic reefs (Goldstein et al. 2016). The combination of the proportion of the population spawning and rate of degeneration of postovulatory follicles provided an estimate of the number of fish spawning and the frequency of spawning. The proportion of spawning females was applied to fish distributions using the same depth stratum categories as in previous analyses (shallow-shelf calculations were applied to 1–20 m) due to data availability in mid-shelf habitats.

Weekly reproductive output during peak reproduction, ~7 d following the full moon in the summer months (Schmale 1981, Robertson et al.

1988), was calculated using the combination of female fish density, depth-specific size distributions, and the depth-specific frequency of spawning using proportion of females spawning and follicle reabsorption rates. Regional reproductive output was extrapolated to stratum and sub-region estimates based on total reef area using the same methods described for female fish density calculations. Regional error bars were based on density prediction intervals and were modified using the same arithmetic manipulations as predictions. Upper and lower limits do not reflect compounded error associated with such additional calculations. All analyses were implemented using R version 3.2.4 (R Core Team 2016).

RESULTS

Population distributions

Hurdle model results revealed that while there was some variability in fish distributions between time periods, there were predominant consistencies in the relationships among fish density, depth, and location across time periods (Table 1). For all time periods and habitat types, the best-fit models for juvenile fish had a polynomial depth term (Table 1) that indicated lower population densities in the shallowest and deepest habitats and peaks at mid-depths within each habitat type (Fig. 3A). Juvenile model results also consistently showed an interaction between depth and location in reef habitats (Table 1), indicating a general pattern of increasing density from PR to the UK but changes in the degree to which depth affects densities across the study region (Table 1, Fig. 3B).

For adult fish, lower densities in the shallowest and deepest reef habitats were evident across time periods. Most time periods also had an interaction between depth and location in reef habitats, indicating that the relationship between population density and depth varies slightly across the study region, but typically peaks at mid-depths (Table 1, Fig. 3C). From 2009 to 2013, the focal years for reproduction analyses, densities in reef and patch reef habitats increased from PR to the UK (Fig. 3D) and peaked at the mid-depth ranges in patch reef and reef habitats (Fig. 3C). In comparison with juvenile bicolor damselfish, adults were rare in rubble habitats and population densities reached their maxima in slightly deeper habitats than juveniles (Fig. 3A, C).

Table 1. Hurdle model results for bicolor damselfish density (fish 0.04/km²), depth (D), and linearized location (L) for four separate time periods for juvenile and adult bicolor damselfish.

Time period	Age group	Habitat	Model		w
			Count	Binomial	
2000–2002	Juvenile	Reef	$D \times L + D^2$	$D + L + D^2$	0.51
		Patch	$D + L + D^2$	$D + L + D^2$	0.73
		Rubble	$D + L + D^2$	$D + L + D^2$	0.73
	Adult	Reef	$D \times L + D^2$	$D \times L + D^2$	1.00
		Patch	$D \times L + D^2$	$D + L + D^2$	0.71
		Rubble	$D \times L + D^2$	$D + L + D^2$	0.65
2003–2005	Juvenile	Reef	$D \times L + D^2$	$D + L + D^2$	0.54
		Patch	$D + L + D^2$	$D + L + D^2$	0.49
		Rubble	$D \times L + D^2$	$D \times L + D^2$	1.00
	Adult	Reef	$D + D^2$	$D + L$	0.57
		Patch	$D \times L + D^2$	$D \times L + D^2$	1.00
		Rubble	$D + D^2$	$D + D^2$	0.52
2006–2008	Juvenile	Reef	$D \times L + D^2$	$D + L + D^2$	0.67
		Patch	$D \times L + D^2$	$D + L + D^2$	0.70
		Rubble	$D + D^2$	$D + D^2$	0.35
	Adult	Reef	$D \times L + D^2$	$D \times L + D^2$	1.00
		Patch	$D + L + D^2$	$D + L + D^2$	0.72
		Rubble	$D + L + D^2$	$D + D^2$	0.66
2009–2011 (Florida Keys) 2012–2013 (Pulley Ridge)	Juvenile	Reef	$D \times L + D^2$	$D \times L + D^2$	1.00
		Patch	$D + L + D^2$	$D + L + D^2$	0.66
		Rubble	$D + L + D^2$	$D + D^2$	0.38
	Adult	Reef	$D \times L + D^2$	$D + L + D^2$	0.42
		Patch	$D + L + D^2$	$D + L + D^2$	0.40
		Rubble	D	D	0.70

Notes: Hurdle models were fit using a binomial distribution with a logit link for the occurrence portion of the model and a negative binomial distribution for the count component. Models were fit using the square root of depth (D). The full model included a polynomial depth term (D^2) and the interaction between the square root of depth and location ($D \times L$). The table shows the best-fit models selected using Akaike information criterion (AIC). (w) is the Akaike weight comparing the selected model to the set of candidate models that were within $2 \Delta AIC$ (Burnham and Anderson 2002).

Comparison of the logistic and count components from the 2009 to 2013 hurdle model results showed similar underlying patterns of occurrence and density across depths. In reef habitats, adult fish occurrence peaked at ~20–40 m and decreased to under 50% in the deepest habitats (Fig. 4A) where densities were low (Fig. 4B). Probability of occurrence in rubble habitats, which were primarily restricted to shallow depths, quickly declined with depth. In contrast, density increased with depth; however, based on broad 95% confidence intervals, the model predictions encompassed a large amount of uncertainty in deeper rubble environments where adults were rare (Fig. 4A, B).

Female fish abundance

For density predictions, the mean proportion of female fish was 57% on shallow-shelf reefs, 52% on deep-shelf reefs, and 48% in mesophotic

habitats (Appendix S2). In reef environments, female fish densities were substantially lower at PR compared with all depth strata, followed by shallow-shelf habitats (Fig. 5A). Predicted densities of females found on patch reefs were also low in the shallow-shelf stratum, and across depths, densities in patch reefs were consistently lower than reef habitats (Fig. 5A, B).

The amount of available habitat differed considerably among depths and regions and affected subpopulation sizes. The total area of patch reefs was lower than reef habitat, leading to smaller predicted total numbers of female fish (Fig. 6A, B). Available reef habitat and female fish densities peaked at mid-shelf reefs, leading to the highest predicted fish population sizes (Fig. 6A). In the MK and UK, female abundance was similar in shallow-shelf and mid-shelf reefs and low in deep-shelf habitats (Fig. 6A). In the LK, total abundance was highest in mid-shelf reefs. The

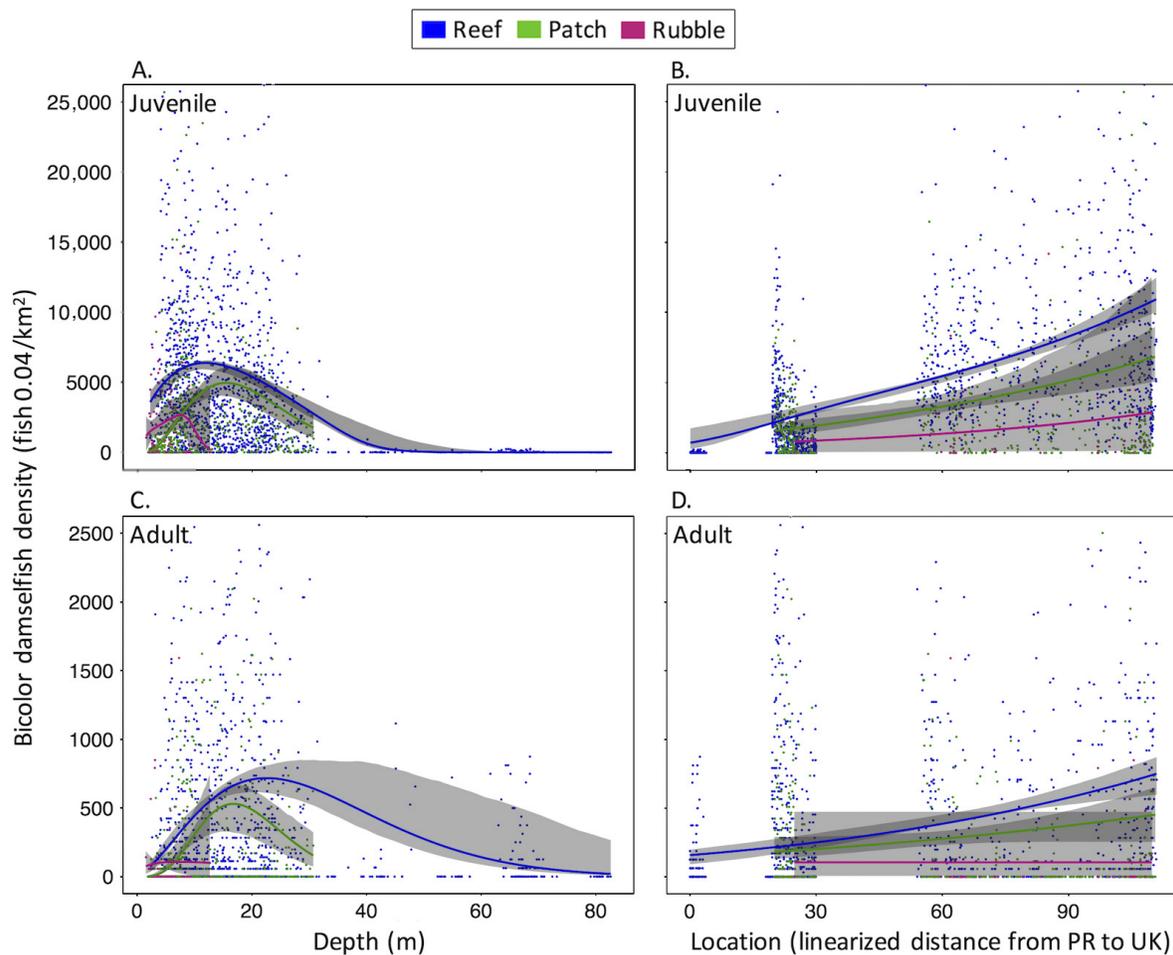


Fig. 3. Representation of hurdle model results that modeled the relationship between the square root of depth, a polynomial depth term, linearized location, and bicolor damselfish juvenile (A, B) and adult (C, D) densities (fish 0.04/km²) for 2009–2011 from the upper Florida Keys (UK), middle Florida Keys (MK), lower Florida Keys (LK), and the Dry Tortugas (DT) visual surveys and 2012–2013 for remotely operated vehicle surveys in the DT and Pulley Ridge (PR). Reef, patch reef, and rubble are designated by color and were modeled separately (Table 1). For plots (A, C) that focus on depth, location was held constant for model predictions at a linearized distance of 70 units. For plots (B, D) that focus on location, depth was held constant at 10 m for model predictions. Note that the y -axis for juvenile plots is an order of magnitude higher than adults, and for ease of visual interpretation, y -axes were truncated such that additional observations that were included in model fits are not visible in the figures. Error bands are bootstrapped 95% prediction intervals based on 1000 replicates for each model.

subpopulation size of female bicolor damselfish at PR is estimated to be approximately the same scale as each subregion in the Keys (Fig. 6A). Summing all strata and subregions in the Florida Keys provided a total Keys-wide female bicolor damselfish population in reef habitats of 2,003,607. Based on these conservative estimates of reef area at PR, the total number of female

bicolor damselfish is 333,000 or approximately 17% of the number of female fish over the entire extent of reef habitat in the Florida Keys.

Egg production

Population demographic calculations were made for only reef habitat based on the large spatial extent and high numbers of bicolor

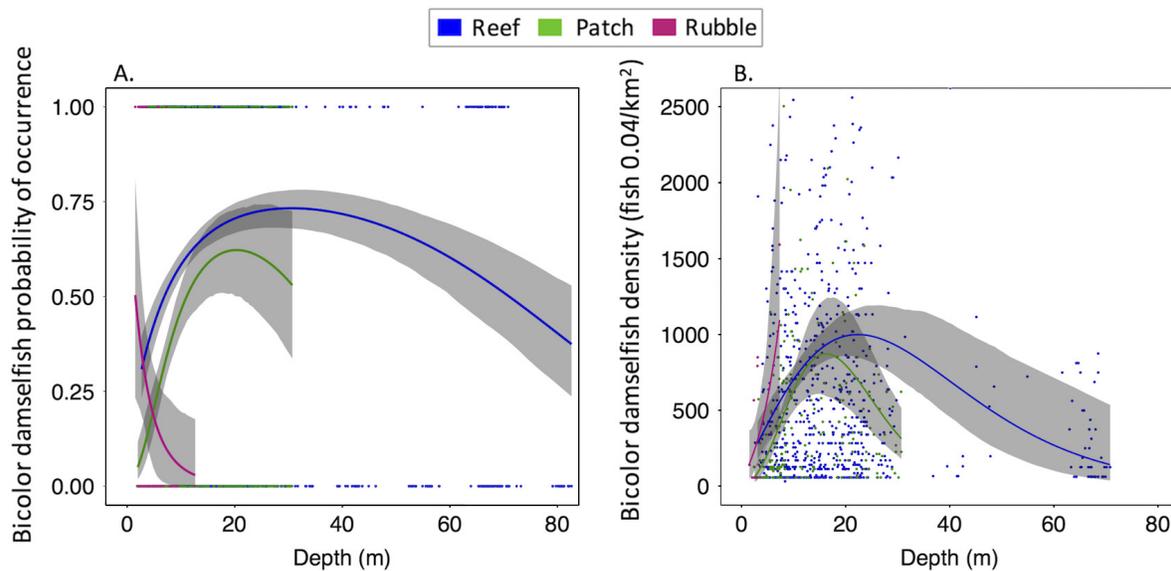


Fig. 4. Predicted (A) presence/absence and (B) negative binomial count components from hurdle model results for adult fish surveyed from 2009 to 2013 (Table 1). Location was held constant at 70 units for the graphical model depiction. Error bands are bootstrapped (1000 replicates) 95% confidence intervals calculated based on model coefficients. Color corresponds to benthic habitats. For ease of visual interpretation, the y -axis for the negative binomial portion of the model (B) was truncated such that additional observations that were included in model fits are not visible in the figures.

damselfish in reef habitats compared with rubble (Fig. 3C) and patch reefs (Fig. 6B). Female fish length distributions shifted from smaller individuals in shallower habitats, to a higher frequency of larger size fish as depth increased (Fig. 7). Predicted reproduction echoed the underlying relationship between fish density and depth (Fig. 8); however, differences in the proportion of spawning females had a large impact on predicted weekly egg production. Reproductive output estimates in deep-shelf and mesophotic habitats (Fig. 8) were lower than in mid-shelf reefs despite larger body sizes and higher fecundity in the deepest habitats. Predicted weekly egg production for each km^2 of reef habitat, grouped by subregion and depth stratum, indicated high egg production in mid-shelf habitats, followed by deep-shelf habitats and shallow-shelf habitats, and the lowest egg production/ km^2 in mesophotic environments (Fig. 8).

On a regional spatial scale, reproduction peaked at mid-shelf and shallow-shelf habitats in the MK and UK and mid-shelf habitats in the LK as a result of high population densities and availability of reef habitat (Fig. 9). The magnitude of

total potential reproductive output at PR was similar to subregions and depth strata in the Florida Keys. The total population in the Florida Keys potentially produces ~ 10 times more eggs during weekly peak reproduction periods in the summer months compared with PR. Based on these analyses, of the total number of bicolor damselfish eggs produced over the entire region, $\sim 9\%$ are sourced from mesophotic populations at PR.

DISCUSSION

We utilized data from several sources to assess the influence of spatially explicit depth-stratified population density, demographics, and habitat availability on subregional reproductive output of a coral reef fish from their ostensibly preferred depths to the boundaries of coral reef ecosystems. Our results indicate that spatially variable subpopulation demographics and dynamics have major implications for reproductive output. These findings can be used to refine biophysical models that are essential to assessing population connectivity and ecosystem management. Additionally, estimates of population size and

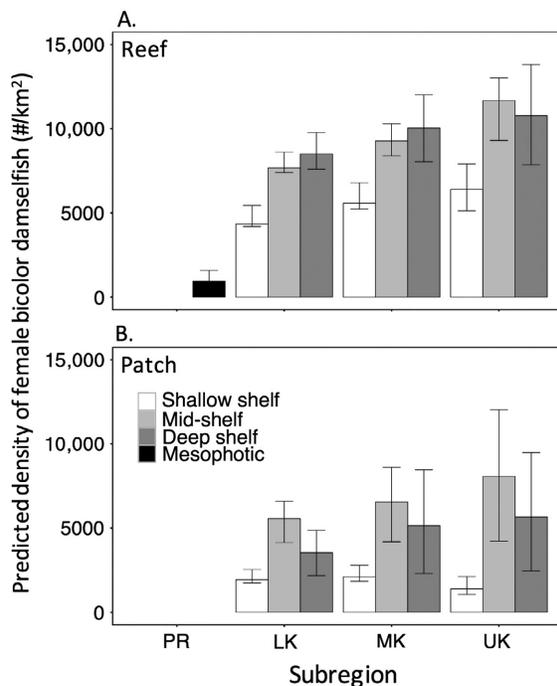


Fig. 5. Predicted density of bicolor damselfish during the time period from 2009 to 2013 at Pulley Ridge (PR) and the Florida Keys for (A) reef and (B) patch reef environments within depth stratum and subregion (LK, lower Florida Keys; MK, middle Florida Keys; UK, upper Florida Keys; PR, Pulley Ridge). Depth strata were defined as shallow shelf <10 m, mid-shelf 10 to <20 m, deep shelf 20 to \leq 30 m, and mesophotic 60–90 m. Error bars were calculated from bootstrapped 95% prediction intervals from hurdle model results for adult bicolor damselfish.

reproductive output provide insight into the ecosystem value and function of peripheral habitats and the capacity for deep-shelf and mesophotic reefs to function as refuges by supplying larvae to degraded shallow reefs.

Population distributions

Along a depth gradient, bicolor damselfish populations had an underlying temporal and spatial pattern of low density at the tail ends of the depth distribution and maximum densities at the middle range. This distribution indicates that bicolor damselfish are found across a broad depth range in coral reef habitats with some restrictions on their occurrence and abundance in peripheral environments. Juvenile bicolor damselfish

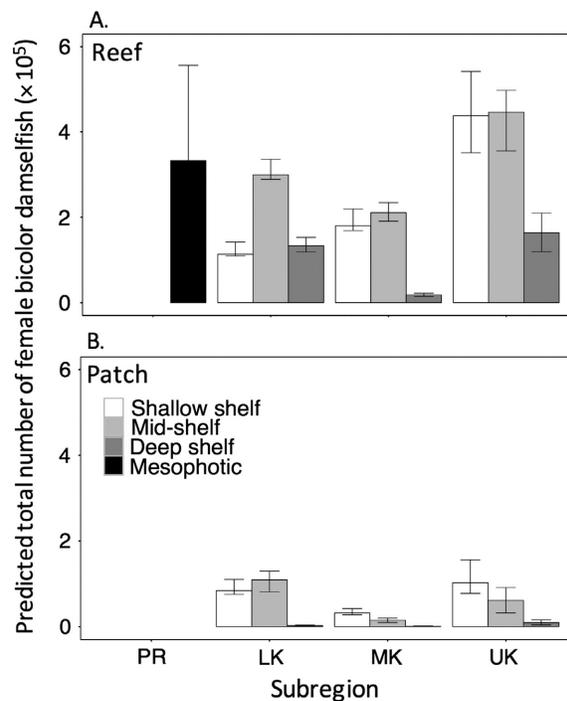


Fig. 6. Predicted total number of bicolor damselfish females at Pulley Ridge (PR) and in the Florida Keys for (A) reef and (B) patch reef environments within depth stratum and subregion for 2009–2013 (LK, lower Florida Keys; MK, middle Florida Key; UK, upper Florida Keys; and PR, Pulley Ridge). Depth strata were defined as shallow shelf <10 m, mid-shelf 10 to <20 m, deep shelf 20 to \leq 30 m, and mesophotic 60–90 m. Error bars were calculated from bootstrapped 95% prediction intervals from hurdle model results for adult bicolor damselfish. For PR, total female bicolor damselfish population size was calculated based on an estimated reef area of 350 km² (area of the HAPC, Habitat Areas of Particular Concern).

distributions are skewed toward shallower habitats in comparison with adult distributions that coincide more closely with the center of the depth range of coral ecosystems within the study region at ~10–30 m. Restrictions to population densities along clines are common across ecosystems (Brussard 1984) and can be regulated by processes such as dispersal (Guo et al. 2005), recruitment (Jones 1990, Forrester 1995), mortality (Forrester et al. 2008, Hixon et al. 2012), habitat availability (Serafy et al. 2015), and survival and growth trade-offs throughout ontogeny (Srinivasan 2003). The slight shift in depth distribution

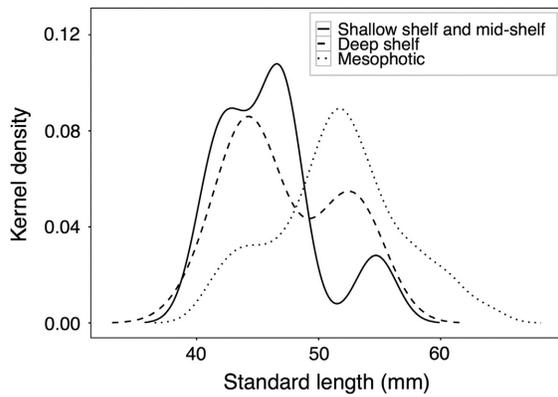


Fig. 7. Kernel density size (standard length) distributions of adult bicolor damselfish females from shallow-shelf (also used for mid-shelf distributions) and deep-shelf habitats in the Florida Keys, and mesophotic reef collections from Pulley Ridge. Data were adapted from Goldstein et al. (2016).

toward deeper environments for larger individuals suggests that multiple processes may be regulating population demographics and distributions across depths. While bicolor damselfish are very common in the Florida Keys, there is evidence that variation in population densities

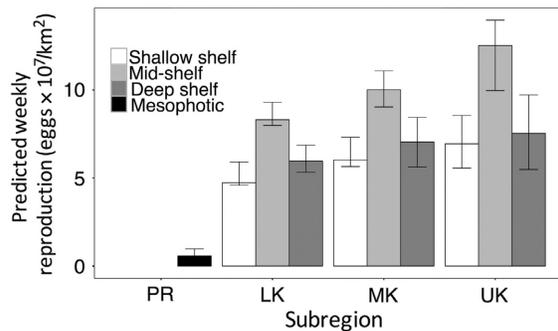


Fig. 8. Predicted bicolor damselfish weekly reproductive output (number of eggs/km²) across depth strata and regions from 2009 to 2013 for lower, middle, and upper Florida Keys (LK, MK, UK, respectively) and Pulley Ridge (PR). Error bars were derived from bootstrapped 95% prediction intervals of hurdle model predictions and then modified based on depth-specific spawning proportions and spawning frequency. Depth strata were defined as shallow shelf <10 m, mid-shelf 10 to <20 m, deep shelf 20 to ≤30 m, and mesophotic 60–90 m.

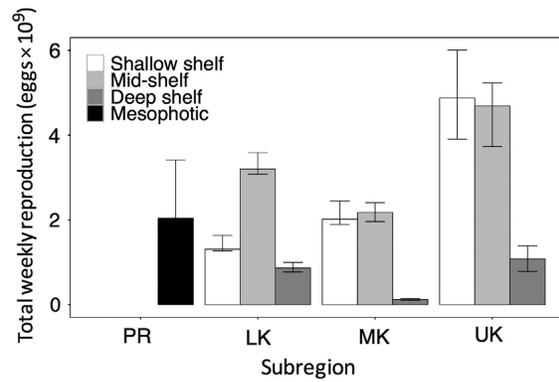


Fig. 9. Predicted bicolor damselfish weekly reproductive output (total number of eggs per week) for the total area of reef habitat across depth strata and subregions from 2009 to 2013 for the Florida Keys (LK, lower Florida Keys; MK, middle Florida Keys; UK, upper Florida Keys) and Pulley Ridge (PR). Error bars were derived from bootstrapped 95% prediction intervals from hurdle model predictions and then modified based on depth-specific spawning proportions and spawning frequency. Depth strata were defined as shallow shelf <10 m, mid-shelf 10 to <20 m, deep shelf 20 to ≤30 m, and mesophotic 60–90 m. For PR, values were calculated based on 350 km² of reef habitat (approximate area of the HAPC, Habitat Areas of Particular Concern).

across geographic locations and depths may be linked to differential replenishment and postsettlement mortality of young fish (Sponaugle et al. 2012; Goldstein et al. 2016). Ultimately, density distributions demonstrate that mid-shelf reefs support dense populations of juvenile and adult demersal reef fish in comparison with habitats that are near their distributional boundaries.

Probability of occurrence revealed patterns in adult distributions that were not detectable based on densities alone. In reef habitats, occurrence of adults remained high, dropping from a peak of ~75% to just below 50% in the deepest habitats. In contrast, densities dropped by an order of magnitude from mid- to mesophotic depths. There is evidence that individual damselfish are less aggregated in continuous habitats compared with patchier environments (Levin et al. 2000). Bicolor damselfish may aggregate at high population densities in the most complex shallow-reef habitats, and have a more dispersed distribution in deeper reef habitats that are more uniform in

complexity. Clustered or patchy fish distributions lead to a lower frequency of occurrence if the scale of sampling is sufficient to capture the variation. In deeper habitats dominated by continuous reefs and low-relief spur and groove (Appendix S1), fish distributions tend to be more uniform with a high frequency of occurrence, but at lower densities than those in more variable shallow habitats.

Bicolor damselfish frequency of occurrence also differed across depths and age groups in patch reef and rubble habitats that are primarily restricted to shallow depths in the Florida Keys (Lidz et al. 2006). High frequency of occurrence on patch reefs in deeper habitats may be linked to habitat configuration or settlement cues to isolated habitats (Morton and Shima 2013). Adult bicolor damselfish were rare in rubble environments, whereas juveniles were common in shallow-water rubble habitats that provide shelter from predation for small fish (Nemeth 1998). These results indicate that rubble may be an important habitat for young fish that is not available on deeper reefs, suggesting that habitat preference or mortality may contribute to fewer young bicolor damselfish and lower fish densities in mesophotic reef environments (Goldstein et al. 2016).

Female fish abundance

The combination of population densities, frequency of occurrence, and sex ratios of bicolor damselfish led to broadscale distribution estimates of female fish across regions and depth strata. Regional patterns mirrored the shape of continuous density distributions, with the highest densities of female bicolor damselfish found in mid- and deep-shelf habitats. The estimated density of female fish in mesophotic habitats at PR indicated substantially lower densities than shallower reefs despite the high proportion of individuals of reproductive size and age in deeper environments.

The amount of available reef habitat for bicolor damselfish populations varied considerably among depths and regions. The total subpopulation number of female bicolor damselfish was largely driven by differences in available habitat. Notably, deep-shelf reefs had the smallest total population sizes in the Florida Keys. Reef habitat in the Florida Keys declines between 30 and 35 m until a secondary outlier reef is reached at

~45 m (Lidz et al. 2003), limiting the total area of deep-shelf habitat available to demersal reef fish. Mid-shelf reefs supported high densities of fish and provided the most extensive reef habitat, resulting in the highest population sizes. Patch reef fish populations reached densities that were comparable to other habitats, but the total area of patch reefs is minimal in the Keys, with substantially lower numbers of female bicolor damselfish compared with more continuous reefs.

Mesophotic reefs likely encompass a large expanse of benthic habitat for reef fish. Although PR is less thoroughly mapped than the Florida Keys, ROV surveys confirmed that reef habitat at PR extends to a flat basin and secondary ridge to the west of the ridge crest (Jarrett et al. 2005, Reed et al. 2014). Based on conservative estimates of total reef area, the population size of female bicolor damselfish at PR is substantial, comprising 14% of the total number of female fish found in the entire study region. A large population size suggests that despite low population densities, PR and other mesophotic reefs may be important reef habitats for demersal coral reef fish.

Egg production

Potential reproductive output, measured as egg production or population fecundity, is the result of a combination of population size, or spawning stock biomass, individual fecundity, and frequency of spawning. Fine-scale differences in fish populations, such as body size, can mediate reproductive output, and the positive relationship between fish body size and fecundity observed for bicolor damselfish (Goldstein et al. 2016) is well documented across species (Hixon et al. 2013). Larger parental body size also provides more subtle advantages to offspring including increased condition and survival in the planktonic environment (Berkeley et al. 2004, Marshall et al. 2010). Batch fecundity, oocyte area, and female body size increase with depth, indicating that for each spawning event, females from deeper habitats produce both more larvae per capita and larvae of higher condition than those from shallower habitats (Goldstein et al. 2016).

Reproductive output was driven by variation in female fish densities across depth strata, but additional depth-related differences in demographics,

spawning frequency, and fecundity altered the underlying patterns. Mid-shelf peaks in reproductive output were even more striking than differences in female densities. Despite larger body sizes creating the potential for increased per capita reproductive output, fewer female fish spawned on deep-shelf and mesophotic reefs (Goldstein et al. 2016), resulting in notable declines in egg production compared with shallow- and mid-shelf habitats. While predicted reproductive output per unit area was markedly lower at PR than in the Keys, increased habitat availability resulted in a total egg production estimate that was ~10% of the total egg production in the Keys.

Reproductive output calculations in this study likely represent a conservative estimate of egg production from mesophotic environments. Fecundity analyses did not account for the influence of density-dependent processes on reproduction that would likely increase reproductive investment in deeper habitats that have lower population densities (Samhuri 2009, Hixon et al. 2012). After accounting for differences in body mass, previous studies revealed high reproductive investment in mesophotic environments compared with shallower habitats; however, factors other than density also likely influence reproduction across depths (Goldstein et al. 2016). Due to the limitations of the available data sets, weight–fecundity relationships across depths could not be incorporated into this study, resulting in a single length–fecundity relationship that does not encompass other measures of reproductive investment. Additionally, spawning frequency was calculated based on probability of spawning using discrete depth bins and temperature-dependent oocyte development linked to spawning frequency. The present study relied on in situ water temperatures from the study period combined with temperature-dependent postovulatory follicle degeneration rates from the literature (Ganias et al. 2007; Goldstein et al. 2016). Such calculations presumably capture the influence of temperature on spawning rates, a pattern that is prevalent across species, yet there may be some variability in the relationship between temperature and degeneration rates among species (Ganias 2012). Finally, estimates of total area of reef habitat at PR range from ~200 to 750 km² (Cross et al. 2005, Jarrett et al. 2005, Locker et al. 2010, Reed et al. 2014),

indicating that available habitat for fish may be greater than the 350 km² used for this study.

CONCLUSIONS

Subregional reproductive output of a coral reef fish was affected by distributional and population demographic patterns, indicating that spatially explicit data that incorporate local demographics can be used to refine and improve population connectivity models, stock assessment for commercially important species, and to determine habitat value for marine fish. Mid-shelf reefs supported high densities of bicolor damselfish, had the highest area of suitable habitat, and as a consequence, were the source of the highest reproductive output in the Florida Keys. While total population size and reproductive output at PR were lower than in the Florida Keys, mesophotic reefs supported ~14% of the female bicolor damselfish across the entire study region and ~9% of the egg production, primarily as a result of expansive reef habitat. Populations at PR were dominated by large adult fish, indicating that mesophotic fish may represent a long-lived, stable population of fecund female fish that may also produce high condition larvae (Goldstein et al. 2016). Subpopulations of bicolor damselfish in potentially marginal habitats at PR may be an important source of larval supply for the Florida Keys and the DT given the prevailing currents and likelihood for larval connectivity across the spatial scale of the study region (Purcell et al. 2009, Qian et al. 2015). While source–sink dynamics are driven by a balance of multiple processes, there is evidence that production and recruitment can be linked (Cowen 2002, Saenz-Agudelo et al. 2015), suggesting the utility of future studies that utilize reproductive output as an estimate of potential larval production that can refine models of population connectivity and inform estimates and projections of population persistence (Burgess et al. 2014).

Spatial patterns of egg production were driven by variation in population density, but additional parameters such as demographics, frequency of spawning, and habitat availability influenced the scale of reproductive output. The use of spawning stock biomass as a predictor of larval supply and recruitment to fish populations is often debated (Hare 2014), and our results reveal that

population demographics are an important component of reproductive output and larval supply. Although not unexpected, the total area of available habitat had a large influence on potential regional egg production. Broadly, these results suggest that marine reserve design that concentrates on hotspots with high population densities may not be an appropriate approach across habitats, and likely cannot compensate for protecting a larger total area of suitable habitat. These results highlight the need for detailed benthic habitat maps to allow predictions of demersal fish populations, particularly for understudied ecosystems such as mesophotic reefs. Mesophotic coral reef ecosystems, such as PR, have the potential to provide extensive reef habitat for fish populations on a similar scale as their shallow-water counterparts.

Our results underscore the importance of regional and habitat-based analyses for estimating and predicting population sizes, and the effects of spatially variable demographics, density, and habitat on total population egg production. Biophysical modeling efforts that incorporate depth and habitat-stratified reproductive output with physical oceanographic processes to examine population connectivity can help to identify source and sink population dynamics across variable landscapes and habitats. While this approach requires extensive empirical data and is therefore uncommon in many ecosystems or regions, the results of this study illustrate the utility and implications of geographically expansive estimates of fish population size and reproductive output across the entire depth distribution of a species. These estimates demonstrate that demographic patterns that vary across distributions can influence large-scale reproductive output and that mesophotic reef habitats, at the periphery of coral reef ecosystems, can support large reef fish populations that may also be sources of larvae for shallow-reef habitats.

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